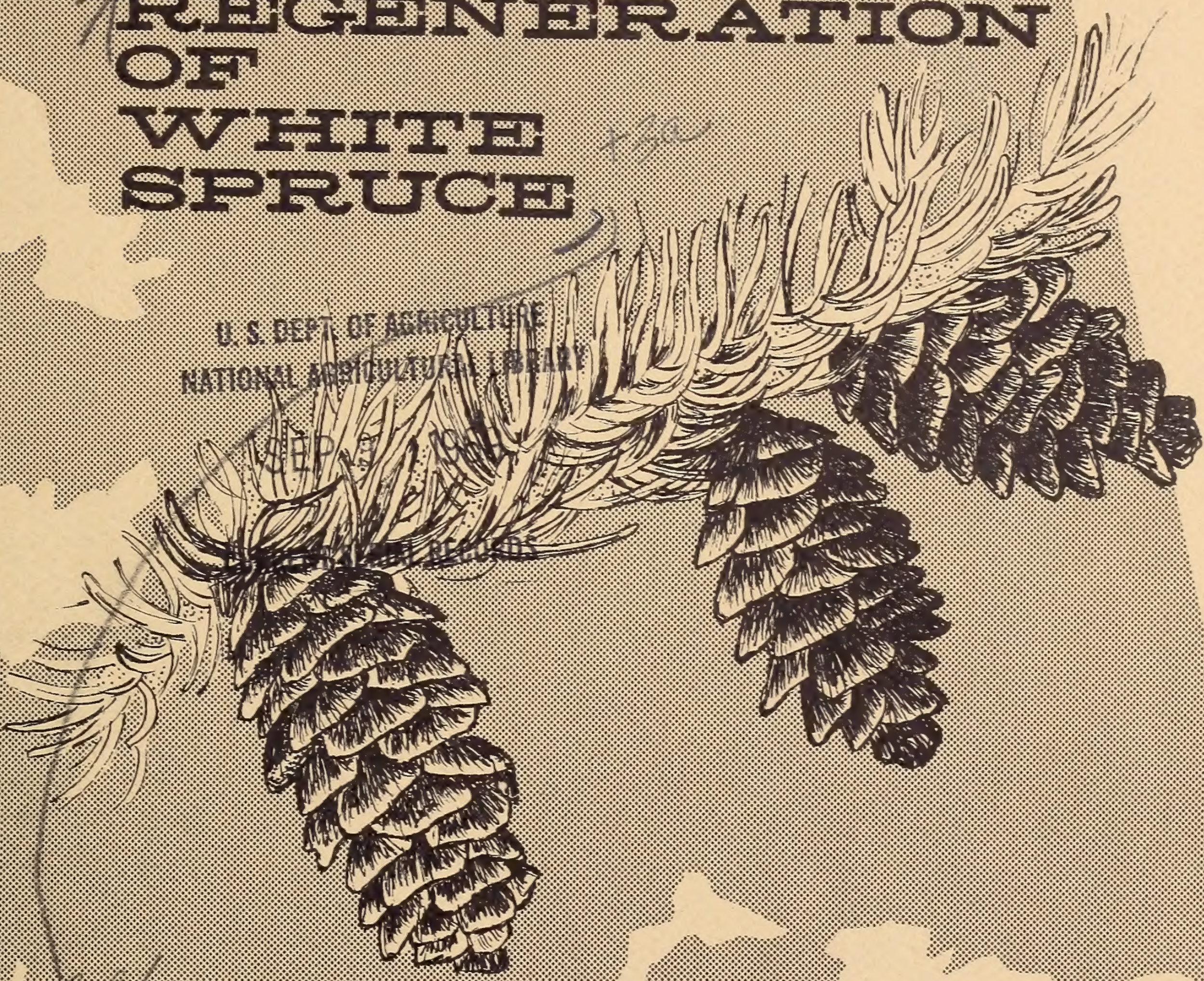
REGENERATION OF WHITE SPRUCE



WITH REFERENCE TO INTERIOR ALASKA;

a literature review

JOHN C. ZASADA
ROBERT A. GREGORY

U.S.D.A. FOREST SERVICE RESEARCH PAPER PNW-79

PACIFIC NORTHWEST FOREST AND RANGE EXPERIMENT STATION
INSTITUTE OF NORTHERN FORESTRY • U.S. DEPARTMENT OF AGRICULTURE
JUNEAU, ALASKA
1969

THE AUTHORS

John C. Zasada is Silviculturist at the Institute of Northern Forestry, Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, College, Alaska.

Robert A. Gregory was Silviculturist at the Institute of Northern Forestry at the time this review was compiled. He is now at Forest Physiology Laboratory, Beltsville, Md.

248142

CONTENTS

INTRODUCTION

White spruce (*Picea glauca* (Moench) Voss) has a transcontinental distribution and grows under a great variety of climatic and site conditions (Nienstaedt 1957). In interior Alaska, which embraces all of the area between the Brooks Range on the north and the Coastal Range bordering the Pacific Ocean on the south (Lutz 1956), white spruce reaches the northern limit of its commercial and botanical ranges. It is the major species in the most important forest type in interior Alaska, covering 57 percent (12.8 million acres) of the commercial forest land (Hutchison 1967).

In interior Alaska, white spruce occurs in even-aged stands and attains its best development along the Tanana River and on the south-facing slopes of the Tanana-Yukon upland (Farr 1967). These stands can be pure or they may contain variable percentages of hardwoods. On the river bottom sites in the Tanana area, soils are relatively coarse textured and the parent material is of alluvial origin. The upland soils are finer textured and generally have formed in loess parent material. The soils on both sites are poorly developed and, under mature stands, they are overlain by a thick organic layer. The growth and yield of these stands has been reported by Farr (1967).

As Alaska develops, the value of the white spruce component of the forest resource will increase. Forest managers wish to maintain the level of spruce growing stock; but in Alaska, as elsewhere, the species does not regenerate easily. The difficulty is due, in part, both to natural factors and to those unfavorable economic conditions which limit the possibility for good logging practices and site preparation.

Because of the difficulty of regenerating this species, a great deal of research has been concerned with solving this problem. Most of the literature reviewed reported the results of research conducted in Canada. All of this work will undoubtedly be helpful in development of practices for obtaining natural regeneration in interior Alaska. However, little of this research has actually been conducted in the forested area of the subarctic; and, although the subarctic resembles other portions of the boreal forest, it differs because of the occurrence of permafrost on some sites, exceptionally long hours of summer daylight, the profound effect of topographic position--especially aspect--on growth, and the relatively short growing season. Literature reporting research conducted in northern Europe on Norway spruce (*Picea abies* (L.) Karst. or *P. excelsa* Link) has been incorporated where appropriate. This is particularly true in the section dealing with seed production.

The purpose of this paper is to present the major results and conclusions reported in the literature, and, where possible, include comparable data concerning interior Alaska conditions. It is hoped that this approach will point out some general requirements which must be met in order to obtain natural regeneration of spruce in Alaska.

SEED PRODUCTION

The Seed Production Cycle

White spruce flower buds form the growing season prior to flowering and can usually be distinguished from vegetative buds in late summer (Nienstaedt 1958; Fraser 1962a; Eis 1967a). Microsporogenesis and megasporogenesis occur early the next spring. At St. Paul, Minnesota (about 45° N. lat.), Winton (1964b) reported microsporogenesis beginning on April 22 and 21 of 1961 and 1962, respectively. Pollen dispersal occurred between 19 and 24 days after initiation of meiosis. However, approximately 100 miles north of St. Paul, meiosis began 2 days later in both years with pollen dispersal occurring 26 to 37 days after initiation of meiosis.

Near Ely, Minnesota (about 48° N. lat.), flowering (female strobili) occurred between May 25 and May 30 over a 4-year period (Nienstaedt 1957). Nienstaedt (1958) found bagged female cones were receptive for a period of from 3 to 5 days in northern Wisconsin.

Over a 5-year period, near Ely, initial pollen shedding varied between May 12 and June 1 (Nienstaedt 1957). Near Fairbanks, Alaska (about 65° N. lat.) during 1958, pollen was dispersed during the last few days of May and in early June; in 1962, pollen dispersal began on June 4 and was essentially completed by June 21 with peak activity between June 6 and 12. In 1968, dispersal occurred between May 31 and June 12. Pollen dispersal has been observed as late as July 11 to 12, north of 53° N. latitude (Nienstaedt 1957).

Development of cones, cone scales, and seeds of white spruce was observed in 1964 in north-central Wisconsin (about 45° N. Lat.) by Clausen and Kozlowski (1965). They reported:

> Whole cones, scales and seeds of white spruce...achieved their highest moisture content of the sampling season, ca. 400 percent, in late May or early June. They showed an overall decrease from this time until reaching their lowest point, less than 40 percent, in September.... Actual moisture content increased early in the season in all determinations and then remained constant until August. It decreased during August when cones of white spruce ...had attained their greatest dry weights.

In Connecticut (about 41° N. lat.), controlled pollinations were carried out between May 9 and 16, 1961. Fertilization occurred in early June, rapid differentiation occurred in July, and the embryos were mature by mid-August (Mergen et al. 1965).

Seed maturity, as measured by the occurrence of germination percentages of seed lots collected prior to natural seedfall not appreciably different from germination percentages found at the time of cone opening, occurs before seed dispersal begins. Crossley (1953) reported that seed could be collected in Manitoba (about 51° N. lat. and elevation 4,500 feet) after the second week in August without sacrificing a great deal in seed viability. Seed dispersal began on September 17 in Crossley's study. In a study conducted at Indian Head, Saskatchewan (about 51° N. lat.), Cram and Worden (1957) reported that in one of their study trees the highest germination percentage occurred in seeds collected about 5 weeks before natural seedfall; in another tree, germination

percentage was greatest 1 week prior to seedfall. Cram and Worden found that a cone moisture content (wet weight) of 48 percent and specific gravity of 0.74 are good general indices of seed ripeness.

Near Fairbanks (65° N. lat.) from 1958 to 1962, cones appeared to ripen about August 20 with seed dispersal beginning shortly thereafter. Peak seed dispersal at Riding Mountain Experimental Forest in Manitoba (51° N. lat.), over a 10-year period, varied from late August to early October (Waldron 1965). At Indian Head, Saskatchewan, natural seed dispersal began, on the average, 98 days after pollen dispersal (Cram and Worden 1957).

Although the majority of seed is dispersed during the year of production, some viable seed has been found in cones the next summer (Roe 1946, Rowe 1953b). Crossley (1955) reported that, during a good seed year in the subalpine region of Alberta, about 88 percent of total seedfall occurred in the first month of dispersal; however, seed continued to fall during the winter, early spring, and as late as May. In northern Minnesota, 22 percent had fallen about 1 month after the beginning of dispersal and 87 percent after about 2 months; 6.5 percent fell about mid-November (Roe 1946).

On the basis of the limited data presented above, it appears that, in general, pollen dispersal occurs later in interior Alaska than farther south. However, it also appears that seed maturation and dispersal occur at about the same time over the species range. This indicates a more rapid development of white spruce seed in the subarctic forests. This more rapid development is in line with the findings of Gregory and Wilson (1968) with regard to the formation of the annual ring in white spruce.

Quantity of Seed Produced

An isolated, open-grown, 75-year-old white spruce in northern Minnesota produced an estimated 271,000 viable seeds from 11,874 cones in a good seed year (Roe 1952). During a heavy cone year in southern Ontario, Tripp and Hedlin (1956) reported an average of over 8,000 cones per tree and 92 seeds per cone of which 25 percent or 23 seeds were sound. Nienstaedt (1958) found an average of 28.3 sound seeds per cone in a sample of cones pollinated in bags. A random sample of 180 cones taken from trees near Fairbanks during the excellent 1958 seed year had 60.5 sound seeds per cone. During a year when only a fair crop of cones was produced, there were 11.4 sound seeds per cone, and in two poor cone years, 6.5 sound seeds (Northern Forest Experiment Station 1960-61).

Table 1 summarizes total seedfall at Riding Mountain Experimental Forest, Manitoba (Waldron 1965), and near Fairbanks (Northern Forest Experiment Station 1960-61).

Factors Affecting Seed Production

The annual variation in white spruce cone and seed crops is great. A moderately well stocked, 170-year-old stand near Fairbanks produced one excellent, one fair, and three poor seed crops from 1957 to 1961. At Riding Mountain Experimental Forest, one good, four moderate, two light, and three nil seed crops occurred between 1954 and 1963 (Waldron 1965). Rowe (1955) reported that, over a 40-year period at Duck Mountain and

Table 1.--*Seedfall at Riding Mountain Experimental Forest, Manitoba, and Bonanza Creek Experimental Forest, Alaska*

(Thousand seeds per acre)

Year	Riding Mountain (100-year-old stand)		Fairbanks (170- 180-year-old stand)	
	Total number of seeds	Total number of sound seeds	Total number of seeds	Total number of sound seeds
1957	14	5	138	86
1958	10	2	16,512	10,733
1959	324	133	123	27
1960	5,625	3,319	--	--
1961	1,409	1,000	--	--

Porcupine Mountain Forest Reserves (about 52° N. lat.) in Manitoba, 12 heavy cone crops occurred. A 30-year record of seed production in southern Finland (about 62° N. lat.) showed that truly good Norway spruce seed years occurred with regularity at the infrequent interval of 12 to 13 years (Sarvas 1957). Uskov (1962) reported abundant seed years in Norway spruce at 3- to 5-year intervals in the northern part of the Vologda Region in Russia (about 60° N. lat.). To understand this variability and how seed production might be increased, one must acquire some knowledge of the factors influencing production.

AGE OF TREES AND STANDS

Cones have been observed on trees as young as 10 years old,[1/] and viable seeds have been obtained from a 13-year-old tree in Maine.[2/] Nienstaedt (1957) mentioned the occurrence of excellent seed crops on 20-year-old, plantation-grown spruce. Stiell (1955) found cones on 20-year-old plantation trees in Ontario and observed that the proportion of cone-bearing trees was greater in more widely spaced stands. He stated that, by age 30 years, 86 percent of the trees in 7- by 7-foot spacing and 42 percent in 4 by 4 spacing were bearing cones. Studies in the mixed-wood forests in Manitoba and Saskatchewan indicated that the beginning of spruce seed production in natural stands occurred at 45 to 60 years of age (Rowe 1955). In Alaska, good cone crops have been observed for trees of this age (45 to 60 years) and for individual trees and stands up to 170 years old.

In general, it appears that, under natural conditions, attainment of a certain minimum crown size and age determines the inception and quantity of flower and seed production in trees (Matthews 1963). Kramer and Kozlowski (1960) stated that most trees produce seed in greatest quantities during middle age, after the

1/ Personal correspondence with Mr. Z. A. Zasada.

2/ Personal correspondence with Mr. A. C. Hart.

period of more rapid height growth has occurred.

WEATHER

Weather at the time of (1) bud setting, (2) flowering, and (3) seed maturation affects seed production and each will be considered below.

Bud Set

Tiren (1935), working with Norway spruce in Scandinavia, concluded that above-average temperatures during June to mid-July of the year of flower bud formation produced high seed yields. A study by Fraser (1958) of the factors influencing spruce flowering in Ontario indicated that hot, dry summers favor flower primordia initiation. In Ontario, MacLean (1959) showed a relationship between seed crops and early spring temperatures of the preceding year; high temperatures were associated with better seed crops. Uskov (1962) reported a significant statistical relationship between the fruiting of spruce stands and the weather (i.e., temperature, precipitation, relative air humidity, and cloudiness) during May, June, and July of the previous year in the northern part of the Vologda Region. The excellent seed year of 1958 in interior Alaska was preceded by an exceptionally hot, dry summer. In correlating weather with seed production of Norway spruce, Sarvas (1957) also observed a favorable effect of abnormally warm or dry seasons seasons, but there were numerous exceptions during the period 1900-55. He emphasized the frequent occurrence of exceptionally high summer temperatures associated with drought, without any subsequent abundant flowering of spruce.

Flowering and Seed Maturation

Concerning weather and flowering, Andersson (1965) stated:

> ...one finds only few data in the literature concerning the effect of the climate and of climatic variations upon the development of floral buds (the meiotic divisions of the micro- and mega-spore mother cells, pollen mitosis and the continued development of the female gametophyte)...

The observation of these phenomena requires exacting techniques and this, perhaps, is one of the reasons for the lack of this information.

The effect of weather on flowering must be considered at least as important as the effect of weather on the formation of reproductive buds. This may be particularly true in subarctic regions. Here, weather conditions at the time of pollen and female gametophyte formation (early to mid-May) may be unfavorable; conditions prevailing at the time of bud formation may be more optimal in any given year. Uskov (1962) stated that a seed crop can be completely destroyed if the frosts are severe enough. He concluded that seed crop periodicity in the northern part of the Vologda Region is often affected by late frosts.

For pine, "A good flowering year is as a rule (though not always) followed by a rich cone crop in the following year but a rich cone year is not always a good seed year" (Andersson 1965). This may also apply to spruce except that the year of flowering and seed dispersal are the same. Destruction of seed during the period of maturation could result from a number of factors. Insect destruction of seed may be of prime importance; however, the effect of adverse weather on seed maturation may also be important. The latter factor has received little attention in the study of white spruce seed production.

POLLINATION

The extent of successful pollination of female ovules is an important factor in determining the quality of white spruce seed crops. Sarvas (1955, 1957) concluded that the high number of empty Norway spruce seed is usually the principal factor reducing seed quality in southern Finland. This is due mainly to incomplete pollination, although some empty seed will occur in spite of sufficient pollination. Nienstaedt (1958) reported that no filled seed developed in unpollinated cones. Both Sarvas (1955, 1957) and Hagner (1958) observed that pollination of spruce flowers remained, as a rule, lower during years when flowering was poor. Nekrasov (1961) reported that supplementary pollination of *P. glauca* produced 49 percent sound seed, whereas naturally pollinated controls gave 12 percent. Navasajtis (1966) stressed the importance of cross-pollination to seed production in white spruce. Mergen et al. (1965) reported that 60 percent of the seed produced in cross-fertilized cones were sound, whereas only 13 percent produced by self-fertilized cones were sound. They found no barrier to self-pollination or self-fertilization; however, self-fertilization often resulted in embryo collapse.

Rain, which created conditions unfavorable for pollination during the period of maximum pollen flight, was the main reason observed by Nienstaedt (1958) for failure of a potentially heavy seed crop of white spruce in northern Wisconsin. Sarvas (1955) stated that during 5 years of observations in southern Finland, rain often delayed the start of flowering or interrupted the spread of pollen for a time, but as a rule its influence was not enough to ruin a potentially good seed year. Wind, stand conditions, and the effect of weather on pollen formation are also important factors in determining the quantity of pollen available for pollination.

LATITUDE AND ELEVATION

Data on the effects of latitude and elevation on the production of white spruce seed were not found. However, this aspect of Norway spruce seed production has received attention in Finland (Sarvas 1957), Sweden (Hagner 1958; Andersson 1965), Bulgaria (Velkov 1965), and Russia (Norin 1958).

In Sweden and Finland, Norway spruce seed production in the north is considerably less than that in the south. Sarvas (1957) has calculated that in the northernmost spruce stands, the seed crops are only about 1 percent as good as the best in central Europe. Hagner (1958) has also observed that spruce cone production declines with increasing elevation; the yield of cones in northern Sweden at 550 meters is about 55 percent of that of 50 meters. Sarvas (1957), Hagner (1958), and Velkov, et al (1965) also found that the number and size of spruce cones and the number of seeds per cone decrease with latitude and elevation. Yet, even at the northern timberline in Finland, filled seed percentage may exceed 70 percent in good seed years. The 1958 white spruce seed crop in Alaska appears to compare very favorably with the number of seeds produced in good seed years in southern parts of the species range (see table 1).

Clark (1961) mentioned extremely slow growth of dwarf trees near the altitudinal and latitudinal tree limits to illustrate a situation where food synthesis appears to barely balance respiratory loss. Simple life functions, such as needle replacement, probably used most of the surplus photosynthate, leaving little for seed production. It seems reasonable to suspect lower seed production at high latitudes and elevations or wherever food synthesis is limited. In fact, a seed-production and seed-quality limit, as well as a vegetation limit, has been observed to exist (Andersson 1965).

Seed Losses

White spruce seed crops are subject to enormous losses before seedfall occurs. A brief discussion of the biological factors important in cone and seed destruction is given below.

INSECTS

Tripp and Hedlin (1956) divided insects that feed on white spruce cones into two groups: (1) "the internals," or those that occupy a restricted environment, with each individual passing its entire feeding period within a single cone; and (2) "the casuals," or those that are not restricted to a single cone, such as some foliage feeders that may also feed on cones. They found the following internal insects in samples of cones from Ontario and Saskatchewan:

Laspeyresia youngana (Kft.)
Pegohylemyia anthracina (Czerny)

Three species of Cecidomyiidae identified as:

Dasyneura canadensis Felt
D. Rachiphaga Tripp
Phytophaga carpophaga Tripp
Megastigmus piceae Rohwer
Two unidentified species of Cecidomyiidae

Among the casual species observed in Ontario and Saskatchewan were:

Dioryctria reniculella (Grote)
D. abietella (D. & S.)
Choristoneura fumiferana (Clem.)
Polychrosis piceana Freeman
Eupithecia togata mutata Pears.

On occasion the casuals are believed to destroy large quantities of cones or seed, but this type of loss is sporadic and difficult to record.

Tripp and Hedlin (1956) concluded that in the vicinity of Ottawa, Canada, the internal insects have been responsible for the destruction of about 28 to 53 percent of the potentially sound seed, depending on the size of the cone crop. During good seed years, the insects become widely dispersed, leaving a large percentage of the cones uninfested; but in light seed years, multiple insect infestations plus many empty seeds result in few or no sound seeds. *Laspeyresia youngana* and *Pegohylemyia anthracina*, may destroy up to 33 and 60 percent, respectively, of the seed crop.

In the vicinity of Anchorage and Fairbanks, Alaska, McCambridge (1957) found *Laspeyresia* spp., Cercidomyiids, and *Megastigmus piceae* in white spruce cones produced in 1954. In a study conducted from 1958 to 1962, in a 300-mile radius of Fairbanks, Werner (1964) found the following cone and seed insects: *L. youngana, M. piceae, Dasyneura canadensis, D. rachiphaga, Phytophaga carpophaga,* and *Pegohylemyia*. He reported,

> Insects damaged 3 - 6% of the seeds per cone during 4 of the 5 years of the study. In 1962, damage increased to 50% and most of it was caused by *Pegohylemia* [sic] sp. Both cone and seed damage was least in 1958 when there was an abundant cone crop and the number of seeds per cone was high. In contrast, the greatest insect damage was in 1962 when few cones were produced but the number of seeds per cone was high.

In northern Wisconsin, Nienstaedt (1957) found only 3.3 percent of the cones bagged during pollination were damaged by insects. Insects damaged 56.5 percent of unprotected, open-pollinated cones.

An extended diapause, according to Tripp and Hedlin (1956), is a characteristic common to many white spruce cone insects. No *Laspeyresia* larvae remained in diapause during a good cone year, but about 40 percent did so when cones were scarce. Thus, year-to-year cone crop variation does not appear to seriously affect survival of cone insects.

DISEASE

Only one disease, the rust, *Chrysomyxa pirolata*, is reported to occur on white spruce cones (Nienstaedt 1957). This rust has been observed on white spruce cones in Alaska by Kimmey and Stevenson (1957). A species of *Chrysomyxa*, probably *C. pirolata*, was very abundant on white spruce over an extensive area south of the Alaska Range in 1960.[3/] During 1968, this rust was present in all stands observed near Fairbanks (north of the Alaska Range).[4/]

Infected cones are said to produce no seed. In 1960, an attempt to collect sound seed from south of the Alaska Range was made difficult because of the high incidence of infected cones. Despite abundant cones, apparently few sound seeds were produced.

SMALL MAMMALS

Red squirrels (*Tamiasciurus hudsonicus*) are common in Alaska and occur over most of the boreal forest region of North America. In Alaska, coniferous seed is an important part of their diet (Brink;[5/] Brink and Dean 1966; Smith;[6/] Streubel[7/]). Captive red squirrels consumed 144 cones per day and can thrive on a white spruce seed diet, but under natural conditions their diets are supplemented with other foods. In captivity, these squirrels preferred white spruce to black spruce (*Picea mariana* (Mill.) B.S.P.) cones (Brink and Dean 1966).

Smith (see footnote 6) has reported that red squirrels are able to thrive on a diet of white spruce buds. During years of cone crop failure, their winter diet may be restricted to buds, which could mean a reduction in the number of potential cones and seeds for the next year.

That squirrels can be considered major consumers of white spruce cones and seed is evidenced by the frequent occurrence of large cone caches (Rowe 1955; Lutz 1956; Wagg 1964a; Streubel, see footnote 7). Streubel reported that, depending on the daily cone consumption rate used in his calculations, squirrels harvested 10 to 69 percent of the cone crop during 1967. He also reported cone caches containing as many as 14,000 cones. During 1957, most of the cones produced during this medium cone year had been harvested by squirrels by the beginning of seed dispersal time.

Red squirrels' cone caches can be a source of seed for silvicultural purposes (Wagg 1964a). However, during the process of cone stripping and seed consumption, squirrels probably scattered little viable seed (Brink and Dean 1966), and they are likely not important as seed dispersal agents.

Artificial Stimulation of Seed Production

Kramer and Kozlowski (1960) stated that a relatively high concentration of carbohydrates appeared to be necessary for the initiation of

---

3/ Identification by T. W. Childs, Forest Pathologist, Pacific Northwest Forest and Range Experiment Station.

4/ Identification by Dr. R. G. Krebill, Forest Pathologist, Intermountain Forest and Range Experiment Station.

5/ Brink, C. H. Spruce seed as a food of the squirrels *Tamiasciurus hudsonicus* and *Glaucomys sabrinus* in interior Alaska. 1964. (Unpublished master's thesis on file at Univ. Alaska, College.)

6/ Smith, M. C. Red squirrel (*Tamiasciurus hudsonicus*) ecology during spruce cone failure in Alaska. 1967. (Unpublished master's thesis on file at Univ. Alaska, College.)

7/ Streubel, D. P. Food storing and related behavior of red squirrels (*Tamiasciurus hudsonicus*) in interior Alaska. 1968. (Unpublished master's thesis on file at Univ. Alaska, College.)

flower buds in forest trees. Numerous methods of stimulating seed production, such as girdling, thinning, and soil fertilization, are aimed at increasing food supply. Girdling restricts downward movement of photosynthates so that food supplies become more abundant in the flower-producing parts of the tree. Thinning and fertilization affect the external factors of temperature, light, soil water, and nutrition; and these, in turn, influence the rates of photosynthesis and carbohydrate accumulation.

Holst (1959) reported that a combination of root pruning, drought, fertilization, and lowering of the auxin level with short-day treatments and antiauxins promoted flowering in white spruce. He also found that white spruce in the ready-to-flower stage can be root-pruned, fertilized with NH_4NO_3, and girdled with good effect. Increased seed yields in other species as a result of thinning, release, fertilization, and other practices indicate that further work in this area may prove valuable in increase of white spruce seed production in selected stands (Matthews 1963).

Seed Crop Prediction

Basically, seed crop prediction aims to provide an accurate estimate of the quantity of seed likely to be produced as early in the production cycle as possible. A sound method of prediction would provide information on which seed collection programs and seedbed preparation could be scheduled to take advantage of seed. Two possible methods of prediction suggested in the literature are discussed below.

Eis (1967a) concluded that a method of prediction based on the abundance of male and female reproductive buds could be developed and would be a useful means of prediction. Early forecasting of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Silen 1967) and western larch (*Larix occidentalis* Nutt.) (Roe 1966) seed crops based on the abundance of reproductive buds has been described. Predictions based solely on the abundance of reproductive buds are of limited use as these observations only indicate the potential which exists under optimal conditions for a good seed year. Observation of cone and seed development subsequent to flowering and fertilization would also be necessary to refine the prediction.

The reported relationship between climatic variables and seed production reported may also be of predictive value. Uskov (1962) has suggested the use of this relationship in predicting Norway spruce seed crops. The relative simplicity of this system makes it attractive. However, reliable data on seed crops from many stands or from individual stands for many years and weather conditions at the time of reproductive bud formation, flowering, pollination, and seed formation are a prerequisite. These data are not available for interior Alaska.

At present, the method of seed crop assessment for white spruce in interior Alaska is based on the presence of mature cones and actual seedfall. No prediction criteria have been developed for interior Alaska.

GERMINATION, INITIAL SURVIVAL, AND SEEDLING ESTABLISHMENT

Germination, early survival, and seedling establishment are three critical periods in the life of a developing seedling. Germination and early survival will be considered jointly in the following discussion because this is commonly found in the literature and because the later stages of germination and initial survival are affected similarly by the same

environmental factors. The period of establishment begins after the seedling has hardened off; however, the period of initial survival is often considered as lasting until the end of the first growing season. Establishment is generally considered as requiring three to five growing seasons after germination, varying with site and seedbed conditions.

Germination and Initial Survival

White spruce germination is epigeal. That is, the primary root elongates first and grows into the soil; the hypocotyl arches upward, pulling the cotyledons into the air where they expand into photosynthetic organs. The seedcoat is shed during this process and the plumule produces a stem bearing leaves (Kramer and Kozlowski 1960).

Seedling shoot and root elongation during the first growing season has been reported by Rowe (1955), Place (1955), Day (1963), Eis (1965) and others. Eis found that, among surviving seedlings, root length averaged 24 millimeters at the end of germination and 52 millimeters at the end of the first growing season; shoot length was 10 and 14 millimeters, respectively. These values will vary with site and weather conditions, but they do give some idea of the size attained by the seedling during the first growing season.

Field germination on mineral soil generally occurs in June and July. For example, at Riding Mountain Experimental Area very little germination occurred in May and the majority (75 percent) in June (Waldron 1966). On 24 mineral soil seedbed plots at Bonanza Creek Experimental Forest (near Fairbanks), 1,300 white spruce seedlings germinated between June 1 and September 1, 1968. Of these, 1,100 (about 85 percent) germinated on or before June 24.

The newly germinated seedling is most susceptible to heat injury during the first growing season and prior to hardening of the hypocotyl when the outer stem tissues die and become dry and straw colored (Smith 1962). This process is caused by the development of the cork cambium. In Douglas-fir, the formation of this lateral meristem may be the most important single development that affects heat resistance (Smith 1958). This tissue develops when the Douglas-fir seedling is 6 or 7 weeks old. No similar data were found for white spruce.

FACTORS AFFECTING GERMINATION AND INITIAL SURVIVAL

Before the specific effects of different seedbeds on germination and initial survival are considered, some general information concerning the effects of temperature, water, and light will be presented. These data, although mostly derived from laboratory tests, indicate why different seedbeds vary in their effect on white spruce seeds and newly germinated seedlings. It must also be stated that the reason for the apparent stress on germination in the subsequent discussion is that the majority of information available pertains to this phase of regeneration and not because it is the most important per se. In fact, as Rowe (1955) stated, the problem of regeneration may not be one of germination as much as of seedling survival.

The seed of white spruce is characterized by embryo dormancy which may be broken by storage in moist sand at 40° F. for 60 to 90 days (U.S. Forest Service 1948), cold-soaking for 20 days at 34° to 38° F. (Crossley and

Skov 1951), or warm-soaking for 24 hours at 70° F. (Wagg 1964b). MacGillivray (1955) found no significant difference in white spruce germination between cold-stratified seed stored for 3 and 14 months. Hellum (1968) reported that cold-stratification adversely influenced germination of the three lots of seed he tested. Heit (1961, 1968) reported that complete germination can also be obtained without pretreatment when light, temperature, and moisture conditions are properly controlled. White spruce seeds have germinated at 35° F. after 1 year or more of stratification (MacArthur and Fraser 1963). Heit (1949) has reported that, in the laboratory, the seed of white spruce did not germinate promptly and completely at temperatures of 68° F. or below. Carmichael (1958) found that the rate of germination of white spruce seed was unchanged by exposure of up to 70 hours at 120° F. and relative humidities (R.H.) up to 30 percent. There was a small reduction at 150° F. and 10 percent R.H. and a great reduction at 20 and 30 percent R.H. A temperature of 180° F. was lethal under all circumstances.

Under field conditions, Rowe (1955) observed a mean air temperature of 44° F. during the week before the first seedlings appeared and a mean of 57° F. during the week in which they formed.

Thiourea substituted for cold treatment in *Picea* sp. (Mayer and Poljakoff-Mayber 1963). Soaking white spruce seed in several concentrations of the potassium salt of gibberellic acid had no effect on its rate of or percent of germination (Grover 1962). Timonin (1966) reported that exposure to ultrasound for 1, 2, or 4 minutes greatly improved the rate of and percent of germination; 6 minutes' exposure was lethal. Vaartaja (1963) found that germination was not affected by extreme pH. Surface sterilization of seed resulted in a significant reduction in germination of white spruce seedlings (Timonin 1964).

Data on temperature optima for seedling growth after germination were not found in the literature. High temperatures can cause seedling mortality by desiccation or by being directly lethal to the seedling. Lethal temperatures may vary to some extent with seedling turgidity but are generally in the 122° to 140° F. range. In moist soil, they may be as high as 158° F. (Day 1963).

Soil water and, in some cases, free water at the soil surface are important to germination and early survival. The first process during germination is the imbibition of water by the seed (Mayer and Poljakoff-Mayber 1963). Waldron and Cayford (1967) reported that germination began at a seed moisture content of 30 percent; at 50 percent, more seed germinated than did not germinate; and at 80 percent moisture content, all seeds germinated. Complete saturation may reduce germination.

Soil water is important to the germinating and developing seedling because it maintains turgidity of the cells and allows metabolic processes to function at rates which insure rapid root penetration to a relatively stable water supply and production of adequate foliage. As mentioned above, turgidity may also be important in determining the susceptibility of the seedling to direct effects of heat.

The importance of light to initial survival is obvious. However, it can also be detrimental when it results in high temperatures and high transpiration rates. The role of light intensity or quality in germination is less obvious. Light treatment of white spruce is beneficial (Jones 1961) and Heit (1968) classifies white spruce as a species requiring light for germination. Sarvas (1950) reported that the seed of Norway spruce germinated much more quickly in light

than in darkness; however, the final result (i.e., percent of germination) was the same. More information is required on this aspect of germination as well as all aspects of the effect of environmental factors on germination and initial seedling survival in white spruce.

Burgar (1964) reported differences between small and large seeds in such factors as total germination, percentage of live seedlings produced, and seedling height at the end of 100 days. Hellum (1966) found a positive relationship between seed weight and both cotyledon number and hypocotyl length. However, he also stated that adverse site conditions may eliminate the influence of seed size on the size of the germinant.

Organic Seedbeds

Raw humus.--Numerous studies have shown that surface organic layers, particularly the thick unincorporated organic layers common to northern coniferous forest regions, are generally very poor or at best, intermediate quality, white spruce seedbeds when compared with other types (e.g., LeBarron 1945; Phelps 1948; Crossley 1952a, 1955b; Parker 1952; Blyth 1955; Place 1955; Quaite 1956; Davis and Hart 1961; Lees 1963; Prochnau 1963; Glew 1963; Wagg 1964a; Eis 1965; Waldron 1966; Jarvis et al. 1966; Hughes 1967). In New Brunswick, Place (1955) found that organic matter accumulations of greater than 2 inches may prevent seedling establishment. Waldron (1966) reported that the effects of organic matter on germination will depend on the depth of the material; on exposed sites, a thin layer of litter may increase germination in dry years. In most cases, one of the major obstacles to successful establishment of white spruce reproduction is the predominance of a raw humus seedbed type.

In reference to soil organic layers, Hawley and Smith (1954) stated:

> ...when kept moist this material makes an excellent medium for germination of most species. The main difficulty is that even in shaded situations it remains moist only when deluged by frequent rains, under the influence of direct sunlight it dries out very rapidly.

Furthermore, increased insolation causes high temperatures at the surface of the organic layer, which is a poor conductor. Eis (1965) recorded temperatures as high as 135° F. and Day (1963) as high as 185° F. Temperatures of this magnitude would be lethal to spruce seedlings.

Rotted wood.--Spruce seedlings often become established in rotting wood; i.e., wood which is well decayed, yet compact (Decie and Fraser 1960). Rowe (1955) stated that, in the absence of any drastic disturbance of the humus layer, rotted wood is the favored surface medium in most stands in the Mixedwood Section of Saskatchewan. Wagg (1964a) and Eis (1965) have also reported the advantage or desirability of rotted wood over humus. Place (1950) showed that the moisture regime of rotted wood is stable and adequate for seedling establishment. On logs and stumps, seedlings are well above the forest floor where they are safe from covering by leaves and, because few other species grow in the medium, they are free from competition (Rowe 1955). Other advantages cited by Rowe are:

1. Improved light conditions--stumps are generally beneath openings in the canopy;
2. Improved temperature conditions--logs and stumps show higher temperatures than the germination layer of the adjacent soils;
3. Less danger of damping off on these seedbeds, and mycorrhizal development is better.

Available evidence indicates how white spruce seedlings, rooted in rotted wood beneath forest stands, are affected by the removal of the forest canopy. Wagg (1964b) stated that, in the Peace and Slave River lowlands, rotted wood may be an important seedbed under stands. But, in clearcuts, the increased temperature and the more rapid drying rate of rotted wood limit seedling establishment. In the subalpine forests of Alberta, hybrid spruce (*Picea engelmannii* X *glauca*) exhibited less mortality on shaded, decayed wood than on a mineral soil seedbed of sandy loam texture (Day 1963). Candy (1951) found excellent coniferous reproduction, which had become established prior to logging, growing on rotted wood in logged areas in the eastern boreal regions of Canada. Moisture conditions are more favorable, however, in eastern than in western boreal regions; and, as pointed out by Candy, this type of reproduction was much less abundant west of Lake Superior.

An interesting role played by rotted wood in white spruce regeneration in the boreal forests of the large river lowlands of western Canada has been reported (Wagg 1964b). Under mature stands, and in the absence of mineral soil, seedlings may become rooted on rotted wood. Alluvium deposited during flooding, which is not detrimental to the seedlings, buries a portion of the seedling's stem and creates conditions under which white spruce is known to form adventitious roots. The alluvium, which is not as susceptible to drying as rotted wood when exposed by overstory removal, assures a more stable source of soil water. This sequence of root development may also be important in similar areas of interior Alaska.

Moss.--Moss seedbeds are common under undisturbed and logged areas in the boreal forest. Generally speaking, this type of seedbed may be favorable for germination early in the growing season, but subsequent survival is poor because of excessive drying. Smith (1962) stated that living mosses can be favorable or unfavorable, depending on whether they grow faster or slower than new seedlings. Johnston[8] reported that black spruce seedlings are often killed by rapidly growing moss.

Place (1955) has reported the effect of different moss species on the germination and survival of spruce and other coniferous species in southern New Brunswick. The following discussion summarizes Place's findings, which may be applicable to interior Alaska.

During wet years, sphagnum moss, on moist but not boggy sites, is not a desirable seedbed. However, during dry years, when adjoining seedbeds are too dry for germination or seedling survival, sphagnum provides an almost ideal seedbed because of its moisture retention characteristics and good aeration.

Polytrichum commune, when growing in low, open stands on dry, sandy soils, creates favorable germination conditions. Dense growths of this species are unfavorable because of low light intensity and because the thick fibrous layer formed by the dead moss prevents the seedling roots from reaching a stable water and nutrient supply. High temperatures and moisture stress, both causes of seedling mortality, are also common under these conditions.

Dicranum rugosum was found to be a moderately favorable seedbed. This species can modify the moisture conditions of its own environment, thus creating relatively favorable conditions for germination and

---

[8] Johnston, W. F. Effect of vegetation and surface condition on artificial reproduction of black spruce in a deforested swamp in north-central Minnesota. 1967. (Unpublished Ph.D. thesis on file at Univ. Mich., Ann Arbor.)

survival. Extreme drying and subsequent high temperatures are not as common with this species as in dense growths of *P. commune*.

Calliergonella (or *Pleurozium*) *schreberi* is generally a poor seedbed for spruce. The species cannot endure direct sunlight and attendant conditions during the summer and usually dies and disappears after logging opens the canopy. Seedlings growing on this seedbed would also suffer mortality. Of the moss species studied by Place, this species provided the poorest seedbed conditions. However, it was more suitable than bare litter. *Hylocomium splendens*, another member of the feather moss group (as is *C. schreberi*), has a similar, or perhaps even more detrimental, effect on spruce regeneration.

Place concluded that the effect of most moss species on regeneration is variable and that the effect of a given species depends a great deal on where it is growing and the density of the moss stand.

Mineral Soil Seedbeds

The majority of data reported in the literature indicated that exposed mineral soil is the most favorable seedbed for germination and early survival of spruce (LeBarron 1945; Phelps 1949, 1951; Parker 1952; Crossley 1952a, 1955a, 1955b; Blyth 1955; Place 1955; Quaite 1956; Ackerman 1957; Weetman 1958; MacLean 1959; British Columbia Forest Service 1961; Davis and Hart 1961; Prochnau 1963; Wagg 1964b; Glew 1963; Jarvis 1966; Eis 1965, 1967a; Jarvis et al. 1966; Scott 1966; Waldron 1966; Hughes 1967; Arlidge 1967). This type of seedbed most closely approximates conditions of a stable, adequate moisture supply, favorable temperatures, and sufficient nutrients. The nature and the arrangement of soil particles also favors intimate contact between the soil water films and the seed.

Although mineral soil is the most favorable seedbed, some detrimental effects have been reported. Heavy soils may become crusted and fissured (MacLean 1959) or baked upon exposure (Gilmour and Konishi 1965). They are also subject to frost heaving (Place 1955). Sandy to sandy loam soils may be too dry for germination in the open (Place 1955; Day 1963). Impairment of physical properties by compaction and reduction of porosity may greatly reduce seedling growth (Weetman 1958). Growth may also be poor on leached A_2 horizons (Place 1955).

Shade

Shade produced by living or dead objects may increase germination and early survival by reducing surface temperatures and evapotranspiration. Day (1963) reported that 40 percent shade reduced mortality in hybrid spruce on all seedbed types tested. In British Columbia, conditions for germination were better under shade; in undisturbed humus, the only seedlings which survived were in the shade of rocks and logs or rooted in rotted wood (Eis 1965). Glew (1963) found the majority of stocked quadrats he observed were not exposed to direct light. Blyth (1955), Place (1955), Prochnau (1963), and others have also reported improved germination and early survival under some degree of shade. Whether shade is produced by living plants or dead objects will only be important if the living plants are also competing with the seedlings for soil, water, and nutrients.

Seedling Establishment

Most white spruce seedling mortality occurs during the first 3 to 5 years after germination (Quaite 1956; Haig 1959; Canada Department of Northern Affairs and Natural Resources 1960;

Prochnau 1963; Eis 1967b). This is generally the period of seedling establishment.

FACTORS AFFECTING SEEDLING ESTABLISHMENT

Seedling establishment is affected by the same factors influencing germination and initial survival as well as by other factors. In some cases, however, the conditions optimal for germination and initial survival may not be the most favorable for seedling establishment and growth. For example, Prochnau (1963) reported that, in general, initial survival was best on mineral soil seedbeds; however, seedling height growth was best on mixed (mineral soil-humus) seedbeds. Although germination is good on rotted wood, seedling growth is extremely slow (Rowe 1955). For example, 20 to 30 years was required for seedlings to reach breast height on rotted wood whereas, on mineral soil, 10 to 15 years was a common age for reaching this height (Rowe 1955). Finally, germination and initial survival are favored by more shade than is optimum for seedling growth. These differences are directly related to the anatomical and physiological changes which occur during seedling development and to the more varied environmental conditions through which the seedling must survive.

The most important factors affecting seedling establishment are soil moisture, light, and nutrient availability and how these are affected by competing vegetation. Other factors which may become important during this period are soil heaving, leaf smothering, and animal and insect damage.

Soil Water and Nutrients

Biotic and abiotic variables are the two sets of factors affecting soil water availability. The abiotic factors consist of the dominating influence of rainfall patterns, physiography, soil, and site. Interior Alaska and the western portion of the boreal forest are characterized by low annual precipitation; in many areas, this is less than 20 inches. Soil water deficits are probably common during the growing season even though this is a relatively wet period of the year. Even on favorable sites, drought may cause some seedling mortality during normal years and excessive mortality during dry years.

Lutz and Caporaso (1958) listed two general site categories in Alaska on which commercial spruce stands do not occur or on which white spruce is absent. Poor tree-soil water relations are among the edaphic variables which limit the growth of spruce on these sites. One of these categories is characterized by a shortage of available soil water. These areas include, among others, oversteepened slopes with south and west exposures and gentler south and west slopes with coarse-textured soils. These areas have probably never supported white spruce.

The second general group of sites is characterized by permafrost near the surface. Attendant with the occurrence of permafrost are such factors as impeded internal drainage, poor soil aeration, and low soil temperatures. All of these factors inhibit root growth. Permafrost occurs most commonly on north slopes and, in these situations, open stands of black spruce predominate.

Permafrost also occurs on potentially productive sites; e.g., in overmature spruce stands in the Chena and Tanana River valleys.[9/] It is in these areas that permafrost may complicate white spruce regeneration.

9/ Dr. L. A. Viereck, personal communication.

Although no research has been conducted concerning the effect of permafrost on regeneration on these sites, it can be concluded from the above-mentioned factors that its effect would probably be detrimental. Extensive disturbance or destruction of the moss layer will be required on these sites to raise soil temperatures, causing the permafrost to recede.

The influence of competing vegetation, the main biotic factor, is superimposed on the abiotic factors. During the period of seedling establishment, the root density of competing vegetation in the surface 10 to 12 inches of soil is critical.

Nutrient supply is extremely important. To date, no work has been completed in Alaska on the relationship between soil fertility and white spruce growth. Field observations indicate that, in some areas, this may be a limiting factor to growth but it may not be as critical during establishment.

Light

Light affects seedling establishment in several ways. First, enough light must be available so that the amount of photosynthate produced is adequate to fulfill normal respiration and minimal growth requirements. If this is not the case, mortality will occur. Too much direct radiation, on the other hand, may limit growth by causing drought.

White spruce is generally categorized as relatively shade tolerant. Place (1955) reported that light intensities below 20 percent of full sunlight can be considered limiting. Eis (1967) found that the rate of height growth of young seedlings under 60 percent of sunlight was twice as great as under 20 percent of light. Intensities greater than 60 percent increased height growth only slightly but did result in better diameter growth. Quaite (1956) observed that seedlings were much more vigorous on scarified plots beneath a partially cut stand than beneath a dense undisturbed stand. This may have been due to greater water availability as well as light intensity differences. High shade--i.e., that produced by a shelterwood overstory--may be less detrimental than low shade--that produced by herbaceous and low, woody vegetation. However, this effect may be related to competition for water and nutrients, too.

Competition

Spruce establishment is hampered by herbaceous and woody species (e.g., Blyth 1955, Crossley 1955a, Rowe 1955, Ackerman 1957, Waldron 1966). This is due to competition for soil water, light, and nutrients. The reproductive characteristics of the competing species and the ecological tolerances of these species, relative to white spruce, are important factors affecting the development and nature of this competition.

Most herbaceous and woody angiosperms reproduce prolifically by suckering or sprouting after the death of the main stem. The sprouts or suckers are able to utilize the parent plant's root system for water absorption and the food reserves stored before death. Vegetative reproduction is common to both birch (*Betula papyrifera* Marsh.) and aspen (*Populus tremuloides* Michx.) but not white spruce. To survive, the spruce seedling must develop its own root system, and it is dependent on stored food reserves in the seed and photosynthate produced by the cotyledons and first needles.

Even when reproduction of all species is accomplished by seed, spruce may be at a disadvantage. For example, good seed years for birch are probably more frequent than for spruce. Seed dispersal for birch is also probably more efficient than for spruce because the seed is lighter.

Most herbaceous plants are also prolific seed producers and are capable of rapid establishment and growth in disturbed areas.

Seedling tolerance of environmental conditions is also important in determining which species will flourish. White spruce is more tolerant than birch or aspen to low light intensities, but does not grow as rapidly as these two hardwood species at high light intensities. Jarvis and Jarvis (1963a) have reported that the growth of Norway spruce was more sensitive to both wet and dry soil than was the growth of European species of birch (*B. verrucosa* Ehrh.) and aspen (*P. tremula* L.). That is, spruce growth under these conditions was reduced relatively more than was the growth of birch or aspen. However, spruce seedlings were the most drought resistant (Jarvis and Jarvis 1963b). Whether these relationships apply to the species of spruce, birch, and aspen in Alaska, at comparable stages of development, is not known. Lutz and Caporaso (1958) have reported that aspen is the most tolerant of interior Alaska species to dry site conditions, and that only white spruce approached it in this respect.

Other Factors

Soil heaving.--Soil heaving on mineral soil seedbeds can cause considerable mortality to seedlings during the period of establishment. The roots are near the surface and soil movement caused by freezing of soil water may damage them mechanically or expose them. Parker (1952) and Place (1955) have reported that this phenomena is most severe on fine-textured and wet soils. Crossley (1955a) found that soil heaving is unimportant as a cause of mortality on scarified seedbeds after seedlings are 3 years old. Rowe (1955) also observed mortality as a result of soil heaving.

Leaf smothering.--Smothering of seedlings by annual leaf accumulation may be the most important cause of mortality where herbs, shrubs, and hardwoods are prevalent (Koroleff 1953, 1954; Rowe 1955; Gregory 1966). Under a mature 80-year-old paper birch stand in Alaska, four growing seasons passed before seedlings were large enough to avoid being crushed or smothered by leaves (Gregory 1966). Gregory concluded "...it appears very unlikely that more than an occasional white spruce can become naturally established beneath a birch stand such as this." Rowe (1955) found that the period of greatest mortality during the first 3 years after germination was from September to May and that much of this mortality was traced directly to smothering by poplar leaves. He suggested that in scarified areas a high, plowed ridge would help reduce smothering because the ridge would remain free of leaf accumulation for a long period.

Animal damage.--Browsing of white spruce seedlings by rabbits has been observed in western Canada during the peak of the rabbit cycle (Rowe 1955). Damage was confined mostly to aspen-covered or brushy areas; little or none was observed on open burns. Rodent damage such as girdling by bark-stripping has also been reported (British Columbia Forest Service 1961). Trampling of seedlings by elk has also been cited as an important cause of mortality at Riding Mountain in Manitoba (Waldron 1966).

Date of germination.--The results of a 4-year study reported by Waldron (1966) showed that slightly more 4-year-old seedlings were formed from June germinants than from July germinants and four times more than from August germinants.

LOGGING AND FIRE

From the previous discussion it can be concluded that the optimum conditions for successful regeneration of white spruce in the boreal forest

consist of the presence of a mineral soil, or at least a mixed, humus-mineral soil, seedbed; some degree of shade, particularly for germination and initial survival; an adequate white spruce seed supply; and a reduction in the density of competing vegetation. In the boreal forest region, logging and fire have been and will continue to be the principal site disturbances preceding the establishment of a new forest. The success or failure of white spruce reproduction will depend on the conditions created by these disturbances.

Logging

Logging of the relatively even-aged white spruce stands in interior Alaska is determined by economic considerations, but is probably best considered as diameter-limit cutting. The residual stand is of variable density and composed of spruce less than 10 to 12 inches in diameter and all of the hardwood component which was present prior to logging.

Little ground disturbance and mineral soil exposure occur in logged areas in this region for one or a combination of the following reasons: (1) There is a thick organic matter layer, (2) equipment which can cause the most ground disturbance is not always used, (3) the ground surface is frozen and snow covered for a large part of the year, and (4) all of the trees are not harvested, consequently much of the ground surface is not subjected to the possibility of disturbance by equipment. In the most heavily cut pure spruce stand in which yarding was accomplished with a small tractor in the summer, mineral soil was exposed on only 2 percent of the area. The unincorporated organic matter was disturbed over 18 percent of the area without exposing mineral soil.

Although Candy (1951) reported favorable reproduction following logging of old-growth stands in the Maritime Provinces, the majority of information indicated that even the most fully mechanized logging operations do not create sufficient disturbance and exposure of mineral soil (e.g., Candy 1951; Blyth 1955; Rowe 1955; Quaite 1956; Glew 1963; Prochnau 1963; Wagg 1964b; Scott 1966; Waldron 1966; Jarvis et al. 1966; Hughes 1967). The situation was summarized by Weetman (1958): "At best reliance on logging disturbance for seedbed preparation of cutovers is a haphazard arrangement which usually results in the effective scarification of only a small percentage of the cutover in an irregular fashion. Its use is generally restricted to summer mechanical logging operations on sites with a shallow humus cover."

Fire

Fire is a common natural occurrence in Alaska and other northern interior forest regions. There are numerous records of extensive fires and it appears that most areas have been burned repeatedly. As described by Lutz (1956), forests of the north are especially susceptible to destruction by fire. He mentions relatively low precipitiation, long hours of sunshine during the summer, and remarkably high air temperatures as "factors increasing the hazard in forests which, by their very nature, are readily flammable."

EFFECT OF FIRE ON WHITE SPRUCE

Most tree species of the boreal forest, especially white spruce, are easily killed by fire. In Alaska, living spruce with fire scars are uncommon and, when encountered, are almost invariably located at the extreme edge of burned areas where the intensity of the fire was low (Lutz

1956). The absence of mature trees in large burns means that, unless regeneration can be accomplished from seed already formed, no white spruce seed source would be available for immediate regeneration.

Successful establishment of spruce reproduction subsequent to severe burning has been noted in the Mixedwood Region of Manitoba and Saskatchewan (Rowe 1955; Phelps 1948), in Alberta (Candy 1951), in Alaska (Lutz 1956), and in Ontario (Scott 1966). Most of the benefits derived from burning probably accrue from destruction of organic matter and consequent exposure of a mineral soil seedbed.

Adverse effects of fire-prepared seedbeds on germination and seedling establishment have been reported. Rowe (1953a), working in southern Manitoba, found that germination on severely burned plots was about 1-1/2 months later than that on severely scarified plots; seeds on the burned plots did not germinate until late summer. Crossley (1955b) and Muri (1955) observed lower stocking of spruce on burned areas in the subalpine regions of Alberta and British Columbia, respectively. In a laboratory experiment, Muri reported that ashes had little effect on germination of Englemann spruce, but that seedling survival on ash-covered seedbeds was about one-half of that on the unburned surface due to damping off. Lutz (1956) stated that, in Alaska, as a result of repeated severe fires, productive forest land may become essentially treeless, supporting herbaceous or shrub communities. Austin and Baisinger (1955) and Tarrant (1956) have reported adverse effects of slash burning on Douglas-fir regeneration.

EFFECT OF FIRE ON SITE CONDITIONS

The effect of fire on site conditions will depend on the site, the intensity of the fire, and the frequency of fire occurrence. One of the more important site variables, with regard to spruce regeneration is the thickness and condition of the organic layer at the time of burning. In commercial white spruce stands, this layer is generally thick (2 to 5 inches), but in stands composed primarily of hardwoods it is relatively thin.

In severe fires, organic layers may be entirely consumed, exposing an altered mineral soil surface. Moist subsurface layers of organic matter usually persist after severe fires, but may be consumed by repeated burning. It was noted by Rowe (1955) that fires almost always consume the entire humus layer over well-drained, light-textured soils, but this occurs less often over moist clays. Lutz (1956) observed complete destruction of unincorporated organic matter most frequently on well-drained, rocky slopes or ridges and around the bases of spruce trees where the forest floor was dry because of interception of precipitation by the crowns. He also noted that destruction of the forest floor to mineral soil varied from 0 to 100 percent in different fires and on different areas within a given burn. His examination of recent burns indicated that deep burning to mineral soil involved about 30 to 40 percent of the surface, even in fires severe enough to kill all trees. Fires are usually most severe in pure conifer stands, becoming less severe as the hardwood component increases.

When organic layers are destroyed and their insulating effect is removed, higher soil temperatures occur within the mineral soil during summer months and soils thaw earlier in the spring and freeze earlier in the fall. In areas where permafrost occurs, the permanently frozen layer is extended downward (Lutz 1956). When the organic layer is not completely destroyed, the increased insolation due to the loss of the forest canopy can cause high surface temperatures because of the blackened, poor conducting surface.

Physical and chemical properties of the soil are altered by fire. A general summary of the findings of several studies is presented. Although study conditions are not comparable, the results indicate some general trends.

1. The total amount of nitrogen on the site decreases after burning (Austin and Baisinger 1955; Uggla 1958; Knight 1966). However, burning may increase the N in the residual material and surface soil (Knight 1966; Zwolinski 1967). Tarrant (1956) reported that light burning stimulates nitrification but severe burning strongly reduces N content of the soil.

Heilman (1966) found that nitrogen, expressed on a volume basis, increased with depth in sphagnum soils (i.e., as mineral soil is approached). He concluded that destruction by fire of the nitrogen deficient moss layers, overlying the layers of relatively high nitrogen content, helps to explain the improvement in productivity and nitrogen availability after burning of sphagnum-dominated forests of interior Alaska.

2. Austin and Baisinger (1955), Tarrant (1956) and Uggla (1958) reported that the available supply of nutrients (phosphorus, potassium, calcium, and magnesium) increased immediately following burning. However, these increases are probably only temporary as these salts may be leached out rapidly (Austin and Baisinger 1955, Uggla 1958; Scotter 1963).

3. Soil acidity is generally decreased by fire (Lutz and Chandler 1946). Scotter (1963) found decreased acidity at 1 and 3 inches in soils on burned-over land. Austin and Baisinger (1955) reported that pH had decreased after 2 years but it had not returned to the preburn level. Tarrant (1954) found that the effect of fire on pH and the rate of change in soil pH following burning was related to severity of burns; the harder the burn the greater the rise of pH and the less rapid the return to normal. Uggla (1958) found that in northern Swedish forests, 25 years passed before pH values were equal to those in unburned areas.

4. Severe burning reduced pore volume and percolation rate below levels in unburned soil (Tarrant 1956). Scotter (1963) reported reduced infiltration rates in a 13-year-old burn, but because of a small number of samples he was unable to draw any definite conclusions.

5. Scotter (1963) reported that soil temperatures at depths of 1 and 3 inches were significantly higher in 5-, 13-, and 22-year-old burns than in unburned areas.

The residual effects of fire may persist for relatively long periods of time in the dry interior of Alaska as Scotter (1963) and Uggla (1958) found for northern Saskatchewan and northern Sweden, respectively.

SILVICULTURAL CONSIDERATIONS

Seedbed Scarification

Because logging and fire do not often result in conditions optimal for the establishment of white spruce, scarification has been used to prepare a seedbed and reduce the density of competing vegetation. Scarification has been shown by a number of investigators to greatly improve seedbed conditions (e.g., LeBarron 1945; Phelps 1948; Crossley 1955a, 1955b; Parker 1952; Blyth 1955; Place 1955; Rowe 1955; Quaite 1956; Ackerman 1957; MacLean 1959; Jeffrey 1961; Lees 1962, 1963, 1964a; Prochnau 1963; Wagg 1964; Gilmour and Konishi 1965; Gilmour 1966; Jarvis et al. 1966; Waldron 1966; Scott 1966; Hughes 1967). The success of this treatment will, however, vary between sites and between years on the

same site (Jarvis et al. 1966, Scott 1966; Waldron 1966). Scarification equipment, methods, and guidelines have been discussed by Weetman (1958), Decie and Fraser (1960), Gilmour and Konishi (1965), Scott (1966), Gilmour (1966), Jarvis et al. (1966), Waldron (1966), and Hughes (1967). The report by Gilmour (1966) of the success of winter scarification followed by seeding may be particularly applicable to interior Alaska conditions.

In the past, scarification has not been widely practiced. This was due to the high cost of treatment, to unfavorable economic conditions, and to disregard of logged and burned areas. The increasing desire to obtain regeneration immediately after harvesting and to regenerate inadequately stocked, burned, and cut areas has made this treatment more common in recent years. For example, in British Columbia (the Prince George Forest District), scarification acreage has increased from 243 in 1956 to 10,000 in 1964. The total area treated up to and including 1964 has been 37,700 acres (Gilmour and Konishi 1965).

The length of time the scarified seedbed remains receptive is important, particularly if natural seedfall, with its inherent annual variation, is relied upon to regenerate a specified area. Most observers report that, depending on site, seedbeds are most receptive for a period of from 3 to 5 years following treatment (Rowe 1955, Crossley 1955a, Lees 1964a, Hughes 1967). A detailed study of this problem in British Columbia reported the following (Arlidge 1967):

1. Scarified areas should be seeded the same year and not later than one growing season after treatment.

2. The size of the seedbed has an important effect; success was lower on small seedbeds than large.

3. Large tractors did a significantly better job than medium or small machines. This was related to the creation of more large seedbeds on areas scarified by large tractors.

Several problems have arisen in connection with use of the treatment. Although they are probably not always important or critical they must be recognized. Depending on the soil type, compaction may result in poorer growth in portions of the treated area. Hughes (1967) and Lees (1964b) report that water retained in depressions created during scarification may reduce seedling growth or cause mortality due to flooding. Lees reported the results of a laboratory experiment which showed that 2-year-old seedlings were more tolerant to immersion than those 1-year-old, and that all 1- and 2-year-old seedlings died after 14 days' immersion. He also found that periods of repeated immersion (3-1/2 to 10-1/2 days) shorter than 14 days had cumulative effects which also resulted in mortality.

Prescribed Burning

The use of fire as a silvicultural tool is important and is increasing in importance in the southeastern United States, the Lake States, Canada, and northern Europe. Because of the role fire has played in forest succession in Alaska and because of its relatively low cost of application, its use should be seriously considered. It is possible that, if the proper burning conditions exist, fire by itself can create an adequate seedbed for spruce regeneration. However, Jarvis and Tucker (1968a, 1968b) concluded that fire alone was not a satisfactory seedbed treatment at the Riding Mountain Experimental Area. They suggested that seedbed treatments combining scarification and burning may prove the most desirable. Effective use of prescribed fire requires data on the effect of fire on site factors and correlation of fire intensity with fuel moisture, fuel type, and weather conditions.

Seed Supply

Even if there is a suitable seedbed, a scarcity of seed may pose an obstacle to regeneration. In selectively logged areas, seed abundance will depend on the quality of the residual trees and their distribution. Waldron (1965) has reported that dominants and codominants produced more cones than intermediate and suppressed trees. Even in heavy seed years, trees in the latter two crown classes produced light seed crops.

In clearcuts, the distance from the uncut forest is of primary importance. The distance of spruce seed dispersal varies with wind, weather, and stand conditions. Some values for this distance have been reported. Rowe (1955) found that 330 feet was the greatest measured distance traveled by seeds, but he stated that seed could be blown farther. MacLean (1959) suggested that clearcut areas be restricted to about 200 feet in width. Hughes (1967) found that seed dispersal in Ontario was not adequate in the middle of a 660-foot-wide clearcut block, and he recommended clearcut strips up to 400 feet wide. The importance of seed blown over snow-covered surfaces depends on the amount of seed shed late in the year. This may not be of major importance in regenerating white spruce. In both clearcuts and selectively logged areas, the quantity of seed produced in a given year will also be important.

The average number of seeds required to establish a seedling varies with site and seedbed. Eis (1967b) reported that, in the Prince George Forest District, one seedling became established for each seven to nine viable seeds on mineral soil, whereas 800 to 1,000 seeds were required on litter. Prochnau (1963), also working in British Columbia, found in a drier than average year that eight viable seeds (protected against rodents) produced one seedling whereas in a wetter than average year four seeds produced one seedling. He concluded that 10 seeds (protected against rodents) per spot are necessary to produce satisfactory results under any conditions. Scott (1966) reported that in Ontario, it is a common practice to use 20,000 seeds per acre when seed is broadcast and six to twelve seeds per spot in spot seeding. These operations are generally conducted on scarified areas and the seed is protected against rodents.

Seed years are generally classified as good, medium, or poor, or by similar adjectives. The adequacy of the quantity of seed during so-described years has been reported. Jarvis et al. (1966) reported that there is seldom a scarcity of white spruce seed in the Mixedwood Forest Section. For Alberta, Quaite (1956) concluded that good seed years do not appear to be necessary to obtain satisfactory stocking of white spruce if a sufficient number of standing stems are left on an area. He reported excellent reproduction after scarification of clearcuts in a medium to good seed year and inadequate reproduction in a light seed year. In the subalpine region of Alberta, Crossley (1955b) found that, if the most receptive seedbed received seed during a light seed year and the seed was subject to normal seed loss, it did not produce a stand that would meet minimum stocking standards 5 years after germination. Because of this he suggests that only a heavy seed crop will satisfy the demands made by forest fauna and still leave enough seed for regeneration. Preliminary data on seed production in interior Alaska indicate that seed production during some years is definitely not adequate for regeneration.

Artificial Regeneration

Although natural regeneration has been and may continue to be the sole means of regenerating white spruce in Alaska, artificial seeding and planting are important means of regeneration in other parts of the boreal forest.

Artificial seeding, accomplished by either broadcast or spot seeding, provides a means of assuring an adequate quantity of seed in an area at any time. However, it is relatively expensive; it requires collection of seed from mature stands and the handling and storage of large amounts of seed. It is not always reliable and successful and, in some cases, seeding has to be repeated. Broadcast seeding does not guarantee that all of the seed will land on a receptive seedbed, and it will probably only be successful following scarification. Parker (1952) concluded that artificial seeding, although producing a greater number of seedlings and earlier regeneration, was of little practical importance and not commensurate with the cost of the operation. This conclusion is questionable with regard to its general applicability.

The destruction of seed by small mammals and insects must be given consideration when artificial seeding is to be used. For example, Radvanyi (1966) found that of 2,000 hybrid white spruce seed, coated with an insecticide and sown in June, 49 percent were destroyed (35 percent by mice, 9 percent by chipmunks, 3 percent by shrews, and 2 percent by insects). Gregory (1966) has reported seed losses believed due to small mammals in Alaska. To reduce these losses seed can be treated with animal repellents such as endrin and Arasan (Prochnau 1963; Scott 1966; Cayford and Waldron 1966).

Planting white spruce seedlings instead of, or in addition to, direct seeding has been suggested, particularly for good sites (Glew 1963; Eis 1966; Hughes 1967; Arlidge 1967). Some of the advantages of planting are that selected genotypes can be used, spacing can be regulated, collected seed is used more efficiently than in artificial seeding operations, the critical periods of germination and initial survival under uncontrolled conditions are bypassed, and the older seedling is better able to compete with fast-growing, herbaceous, and woody vegetation. Because of the rapid growth of competing vegetation on good sites, scarification is desirable. Planting is expensive and is probably of little practical importance in extensive forestry except on extremely good sites. Planting and direct seeding will probably become more important with increasing intensity of management in the boreal forest.

Silvicultural Systems

The applicability of the common silvicultural systems to even-aged spruce management depends upon the conditions created by the system and their suitability for spruce regeneration. Optimum conditions for natural regeneration of spruce have been discussed. In general, they consist of the presence of a mineral soil seedbed, partial shade with not less than 20 percent of full light, an adequate source of seed, and elimination of competition for soil water and light.

Lees (1962, 1963, 1964a), Glew (1963), and Waldron (1966) have concluded that the silvics of spruce suit it to management under a two-cut shelterwood system. For the spruce-aspen stands of Alberta, Lees recommended that the first cut should occur at about age 95 and that it remove up to 60 percent by volume. Seedbed scarification follows the first cut and the overstory should be removed at age 120. This is considered

rotation age in these stands. For stands similar to those at the Riding Mountain Experimental Area, Waldron (1966) suggested a residual stand of 40 to 60 square feet basal area per acre. If possible, the stand should be entirely of spruce but there should be no less than 25 square feet of this species. The balance of the stand would be hardwoods. It is important that the residual spruce be from the dominant and codominant crown classes; these are the best seed producers. As much as possible of the hardwood component should be harvested or poisoned to reduce spruce seedling mortality by crushing. The first cut should be followed by scarification; the second cut would follow seedling establishment. Under the shelterwood system the seedbed treatment must be mechanical, as prescribed burning will kill the residual stand. Increased growth of the residual stems, as a result of release, may make this system desirable in Alaska where sawlog production is, at present, the primary goal. However, too much blowdown and the high cost of the second cut are disadvantages.

Hughes (1967) recommended clearcutting in blocks or strips 330 to 400 feet wide with scarification 2 or 3 years after cutting. Burning and mechanical seedbed preparation are both possible under this system. Direct seeding and planting may be desirable following clearcutting. The advantages of this system would be most fully realized in those areas where utilization is more complete.

BIBLIOGRAPHY

Abbott, H. G., and Hart, A. C.
1960. Mice and voles prefer spruce seed. U.S.D.A. Forest Serv. Northeast. Forest Exp. Sta. Pap. 153, 12 pp., illus.

Abbott, H. G.
1962. Tree seed preferences of mice and voles in the Northeast. J. Forest. 60: 97-99.

Ackerman, R. F.
1957. The effect of various seedbed treatments on the germination and survival of white spruce and lodgepole pine seedlings. Can. Dep. North. Aff. & Natur. Resources Forest. Br. Tech. Note 63, 23 pp., illus.

Addison, J.
1966. Regeneration of spruce. Brit. Columbia Lumberman 50(6): 42-48, illus.

Andersson, E.
1965. Cone studies in Norway spruce (*Picea abies* (L.) Karst.) Stud. Forest. Suecica Nr. 23, 214 pp., illus.

Arlidge, J. W. C.
1967. The durability of scarified seedbeds for spruce regeneration. Brit. Columbia Forest Serv. Res. Note 42, 20 pp., illus.

Austin, R. C., and Baisinger, D. H.
1955. Some effects of burning on soils of western Oregon and Washington. J. Forest. 53: 275-280, illus.

Bean J. L., and Prielipp, D. O.
1961. Insect damage to white spruce cones and seeds--a factor in spruce regeneration. U.S.D.A. Forest Serv. Lake States Forest Exp. Sta. Tech. Note 602, 2 pp., illus.

Berry, A. B.
1964. Effect of strip width on proportion of daily light reaching the ground. Forest. Chron. 40: 130-131.

Brink, C. H., and Dean, F. C.
1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. J. Wildl. Manage. 30: 503-512, illus.

British Columbia Forest Service.
1961. Forest Research Review ended March 1961. Dep. Lands & Forests, Forest Res. Div., 44 pp., illus.

Blyth, A. W.
1955. Seeding and planting of spruce in cutover lands of the subalpine region of Alberta. Can. Dep. North. Aff. & Natur. Resources Forest. Br. Forest Res. Div. Tech. Note 2, 11 pp., illus.

Burgar, R. J.
1964. The effect of seed size on germination, survival and initial growth in white spruce. Forest. Chron. 40: 93-97.

Canada Department of Northern Affairs and Natural Resources.
1957. Annual report of forest research. 78 pp., illus.

____
1959. Annual report on forest research, year ended March 31, 1959. 70 pp., illus.

____
1960. Annual report on forest research, year ended March 31, 1960. Forest. Br. Forest Res. Div., 65 pp., illus.

Candy, R. H.
1951. Reproduction on cut-over and burned-over land in Canada. Can. Dep. Res. Develop. Forest Res. Div. Silvic. Res. Note 92, 224 pp., illus.

Carmichael, Alan J.
1958. Determination of maximum air temperature tolerated by red pine, jack pine, white spruce and black spruce seed at low relative humidities. Forest. Chron. 34: 387-392, illus.

Cayford, J. H., and Waldron, R. M.
1962. Some effects of leaf and needle litter on greenhouse germination of white spruce and jack pine seed. Forest. Chron. 38: 229-231.

____
1966. Storage of white spruce, jack pine and red pine seed treated with Arasan, endrin and aluminum flakes. Tree Planters' Notes 77: 12-16.

Cayford, J. H., and Waldron, R. M.
1967. Effects of captan on the germination of white spruce, jack and red pine seed. Forest. Chron. 43: 381-384.

Clark, J.
1961. Photosynthesis and respiration in white spruce and balsam fir. State. Univ. Coll. Forest. Syracuse, 72 pp., illus.

Clark, J. D.
1960. Cutting practices in western spruce forests. Forest. Chron. 36: 146-149.

__________ Lehrle, L. W., and Smith, J. H. G.
1954. Scarification in Engelman spruce-alpine fir forests. Brit. Columbia Forest Serv. Res. Note 25, 12 pp., illus.

Clausen, J. J., and Kozlowski, T. T.
1965. Seasonal changes in moisture content of gymnosperm cones. Nature 206(4979): 112-113.

Cram, W. H., and Worden, H. A.
1957. Maturity of white spruce cones and seeds. Forest Sci. 3: 263-269.

Crossley, D. I.
1952a. The survival of white spruce reproduction originating from mechanical disturbance of the forest floor. Can. Dep. Resources & Develop. Forest Br. Silvic. Leafl. 63, 4 pp.

____
1952b. White spruce reproduction resulting from various methods of forest soil scarification. Can. Dep. Resources & Develop. Silvic. Res. Note 102, 18 pp., illus.

____
1953. Seed maturity in white spruce. Can. Dep. Resources & Develop. Silvic. Res. Note 104, 16 pp., illus.

____
1955a. Mechanical scarification to induce white spruce regeneration in old cut-over spruce stands. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Tech. Note 24, 13 pp., illus.

____
1955b. Survival of white spruce reproduction resulting from various methods of forest soil scarification. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Tech. Note 10, 9 pp., illus.

____
1956. The possibility of continuous planting of white spruce throughout the frost free period. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Forest Res. Div. Tech. Note 32, 31 pp., illus.

__________ and Skov, L.
1951. Coldsoaking as a pre-germination treatment for white spruce seed. Can. Dep. Resources & Develop. Div. Forest Res. Silvic. Leafl. 59, 4 pp.

Davis, G., and Hart, A. C.
1961. Effect of seedbed preparation on natural reproduction of spruce and hemlock under dense shade. U.S.D.A. Forest Serv. Northeast. Forest Exp. Sta. Sta. Pap. 160, 12 pp., illus.

Day, R. J.
1963. Spruce seedling mortality caused by adverse summer microclimate in the Rocky Mountains. Can. Dep. Forest. Forest. Res. Br. Contrib. 1003, 36 pp., illus.

____
1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. Can. Dep. Forest. Forest. Res. Br. Contrib. 1037, 25 pp., illus.

Decie, T. P., and Fraser, A. R.
1960. Miscellaneous notes on scarification trials, Prince George Forest District, 1956-1959. Brit. Columbia Forest Serv. Res. Div. Res. Note 36, 22 pp., illus.

Dixon, A. C., and Place, I. C. M.
1952. The influence of microtopography on the survival of spruce and fir reproduction. Can. Dep. Resources & Develop. Forest. Br. Div. Forest Res. Silvic. Leafl. 68, 3 pp.

Eis, S.
1965. Development of white spruce and alpine fir seedlings on cut-over areas in the central interior of British Columbia. Forest. Chron. 41: 419-431, illus.

____
1966. Survival and growth of white spruce wildlings and coastal nursery seedlings in the interior of British Columbia. Forest. Chron. 42: 346-349.

____
1967a. Cone crops of white spruce and black spruce are predictable. Forest. Chron. 43: 247-252, illus.

____
1967b. Establishment and early development of white spruce in the interior of British Columbia. Forest. Chron. 43: 174-177.

Farr, W. A.
1967. Growth and yield of well-stocked white spruce stands in Alaska. Pacific Northwest Forest & Range Exp. Sta. U.S.D.A. Forest Serv. Res. Pap. PNW-53, 30 pp., illus.

Fowells, H. A. (comp.)
1965. Silvics of forest trees of the United States. U.S. Dep. Agr. Agr. Hand. 271, 762 pp., illus.

Fraser, D. A.
1958. The relation of environmental factors to flowering in spruce. *In* The physiology of forest trees. Thimann, K. V. (ed.), New York: The Ronald Press. pp. 629-641, illus.

Fraser, D. A.
1962a. Apical and radial growth of white spruce (*Picea glauca* (Moench) Voss) at Chalk River, Ontario, Canada. Can. J. Bot. 40: 659-668, illus.

____
1962b. Growth of spruce seedlings under long photoperiods. Can. Dep. Forest. Forest Res. Br. Tech. Note 114, 18 pp., illus.

Fraser, J. W.
1952. Seed-spotting of conifers under a mixed hardwood stand. Can. Dep. Resources & Develop. Forest. Br. Div. Forest. Res. Silvic. Leafl. 67, 3 pp.

Gilmour, J. G.
1966. Winter scarification and white spruce regeneration, Saskatchewan. Forest. Chron. 42: 167-174.

________ and Konishi, J.
1965. Scarification in the spruce — alpine fir type of the Prince George Forest District. Preliminary evaluation of methods and resulting regeneration. Brit. Columbia Forest Serv. Forest Manage. Notes 4, 21 pp., illus.

Glew, D. R.
1963. The results of stand treatment in the white spruce — alpine fir type of the northern interior of British Columbia. An evaluation of present cutting practices, in terms of regeneration, growth and mortality. Brit. Columbia Forest Serv. Forest Manage. Note 1, 27 pp., illus.

Gregory, R. A.
1966. The effect of leaf litter upon establishment of white spruce beneath paper birch. Forest. Chron. 42: 251-255, illus.

________ and Wilson, B. F.
1968. A comparison of cambial activity of white spruce in Alaska and New England. Can. J. Bot. 46: 733-734, illus.

Grover, R.
1962. Effect of gibberellic acid on seed germination of elm, Scotch pine, Colorado and white spruce. Forest Sci. 8: 187-190, illus.

Haig, R. A.
1959. Result of an experimental seeding in 1920 of white spruce in western Manitoba. Forest. Chron. 35: 7-12.

Hagner, S.
1958. Om koft-och fröproduktionen i svenska barrskogar. (On the production of cones and seed in Swedish coniferous forests.) Rep. Forest Res. Inst. Sweden 47(8): 108-120, illus. (Engl. summary)

Hawley, R. C., and Smith, D. M.
1954. The practice of silviculture. Ed. 6, 525 pp., illus. New York: John Wiley and Sons.

Heilman, P. E.
1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecology 47: 825-831, illus.

Heit, C. D.
1949. Physiology of germination. N.Y. State Agr. Exp. Sta. Annu. Rep. 68: 42-45.

____
1961. Laboratory germination and recommended testing methods for 16 spruce *Picea* species. Ass. Off. Anal. Proc. 51: 165-171.

____
1968. Thirty-five years' testing of tree and shrub seed. J. Forest. 66: 632-634.

Hellum, A. K.
1966. Seed weight and form of germination in white spruce. (Abstr.) Bull. Ecol. Soc. Amer. 47(3): 103.

____
1968. A case against cold stratification of white spruce seed prior to nursery seeding. Can. Dep. Forest. & Rural Develop. Forest. Br. Pub. 1189, 12 pp., illus.

Holst, M. J.
1959. Experiments with flower promotion in *Picea glauca* (Moench) Voss and *Pinus resinosa* Ait. *In* Recent advances in botany. Univ. Toronto Press. pp. 1654-1658.

Hughes, E. L.
1967. Studies in stand and seedbed treatment to obtain spruce and fir reproduction on the mixedwood slope type of northwestern Ontario. Can. Dep. Forest. & Rural Develop. Forest. Br. Dep. Pub. 1189, 138 pp., illus.

Hutchison, O. Keith.
1967. Alaska's forest resource. Pacific Northwest Forest and Range Exp. Sta. U.S.D.A. Forest Serv. Resource Bull. PNW-19, 74 pp., illus.

Jarvis, J. M.
1966. Seeding white spruce, black spruce and jack pine on burned seedbeds in Manitoba. Can. Dep. Forest. Forest Res. Br. Pub. 1166, 8 pp.

________, Steneker, G. A., Waldron, R. M., and Lees, J. C.
1966. Review of silvicultural research — white spruce and trembling aspen cover types, mixedwood forest section, boreal forest region Alberta-Saskatchewan-Manitoba. Can. Dep. Forest. & Rural Develop. Forest. Br. Dep. Pub. 1156, 189 pp., illus.

________ and Tucker, R. E.
1968a. Prescribed burning after barrel scarifying on a white spruce — trembling aspen cutover. Pulp & Pap. Mag. Can. (Nov. 1, 1968): 70-72, illus.

Jarvis, J. M. and Tucker, R. E.
1968b. Drought index as a predictor of moisture content in L and F horizons on an upland white spruce — trembling aspen cut-over area. Can. Dep. Forest. & Rural Develop. Forest. Br. Dep. Pub. 1237, 10 pp., illus.

Jarvis, P. G., and Jarvis, M. S.
1963a. The water relations of tree seedlings. I. Growth and water use in relation to soil water potential. Physiol. Plant. 16: 215-253, illus.

____
1963b. The water relations of tree seedlings. III. Transpiration in relation to osmotic potential of the root medium. Physiol. Plant. 16: 269-275, illus.

____
1963c. The water relations of tree seedlings. IV. Some aspects of the tissue water relations and drought resistance. Physiol. Plant. 16: 501-516, illus.

Jeffrey, W. W.
1961. Origin and structure of some white spruce stands in the lower Peace River. Can. Dep. Forest. Forest. Res. Br. Tech. Note 103, 20 pp., illus.

Jones, L.
1961. Effect of light on germination of forest tree seed. Int. Seed Test. Ass. Proc. 26: 437-452, illus.

Kimmey, J. W., and Stevenson, J. A.
1957. A forest disease survey of Alaska. Plant Dis. Rep., Epidemics and Identification Sect. Suppl. 247: 87-96, illus.

Knight, H.
1966. Loss of nitrogen from the forest floor by burning. Forest. Chron. 42: 149-152, illus.

Koroleff, A.
1953. The influence of leaf litter on spruce regeneration in mixedwoods. Pulp & Pap. Res. Inst. Can., Woodlands Res. Index 91, 16 pp., illus.

____
1954. Leaf litter as a killer. J. Forest. 52: 178-182.

Kramer, P. J., and Kozlowski, T. T.
1960. Physiology of forest trees. 642 pp., illus. New York: McGraw-Hill Book Co., Inc.

LeBarron, R. K.
1945. Mineral soil is favorable seedbed for spruce and fir. U.S.D.A. Forest Serv. Lake States Forest Exp. Sta. Tech. Note 237, 1 pp.

Lees, J. C.
1962. A discussion on white spruce natural regeneration in Alberta's spruce-aspen stands. Empire Forest. Rev. 41: 214-219, illus.

Lees, J. C.
1963. Partial cutting with scarification to Alberta spruce-aspen stands. Can. Dep Forest. Forest Res. Br. Pub. 1001, 18 pp., illus.

____
1964a. A test of harvest cutting methods in Alberta's spruce-aspen region. Can. Dep. Forest. Forest Res. Br. Pub. 1042, 19 pp., illus.

____
1964b. Tolerance of white spruce seedlings to flooding. Forest. Chron. 40: 221-225, illus.

Lutz, H. J.
1956. Ecological effects of forest fires in the interior of Alaska. U.S. Dep. Agr. Tech. Bull. 1133, 121 pp., illus.

__________ and Caporaso, A. P.
1958. Indicators of forest land classes in air-photo interpretation of the Alaska interior. U.S.D.A. Forest Serv. Alaska Forest Res. Center Sta. Pap. 10, 31 pp., illus.

__________ and Chandler, R. F.
1946. Forest soils. 514 pp., illus. New York: John Wiley & Sons, Inc.

MacArthur, J. D., and Fraser, J. W.
1963. Low temperature germination of some eastern Canadian tree seed. Forest. Chron. 39: 478-479.

McCambridge, W. F.
1957. A record of spruce cone insects in Alaska. Alaska Forest Res. Center Tech. Note 34, 2 pp.

McConkey, T. W.
1964. Direct seeding of pine and spruce in southwestern Maine. Northeast. Forest Exp. Sta. U.S.D.A. Forest Serv. Res. Pap. NE-24, 13 pp., illus.

MacGillivray, H. G.
1955. Germination of spruce and fir seed following different stratification periods. Forest. Chron. 31: 365.

MacLean, D. W.
1959. Five-year progress report on project RC-17. Pulp & Pap. Res. Inst. Can. Woodlands Res. Index 112, 142 pp., illus.

Matthews, J. D.
1963. Factors affecting the production of seed by forest trees. Forest. Abstr. 24(1): i-xiii.

Mayer, A. M., and Poljakoff-Mayber, A.
1963. The germination of seeds. 236 pp., illus. New York: The Macmillan Co.

Mergen, F., Burley, J., and Furnival, G. M.
1965. Embryo and seedling development in *Picea glauca* (Moench) Voss after self-, cross- and wind-pollination. Silvae Genet. 14: 188-194, illus.

Mullin, R. E.
1963a. Growth of white spruce in the nursery. Forest Sci. 9: 68-72, illus.

______ 1963b. Planting check in spruce. Forest. Chron. 39: 252-259.

______ 1964. Reduction in growth of white spruce after out-planting. Forest. Chron. 40: 488-493, illus.

______ 1967. Root exposure of white spruce nursery stock. Forest. Chron. 43: 155-160.

Muri, G.
1955. The effect of simulated slash burning on germination, primary survival and top-root ratios of Engelmann spruce and alpine fir. Univ. Brit. Columbia Forest. Club Res. Note 14, 7 pp.

Navasajtis, M. Z.
1966. (Biology of flowering and seed-bearing of *Pseudtsuga taxifolia* var. glauca and *Picea glauca* in Lithuania) Liet. TSR Mokslu Akad. Darb. (Ser. C) 1966(2): 3-20. (In Russian.) (Forest. Abstr. 28(3): 430 (35067).)

Nekrasov, V. I.
1961. (Using supplementary pollination to increase yields of viable seed of *Picea glauca*) Bjull. Glavn. Rot. Sada Moskva No. 42(54-7). (In Russian.) (Forest. Abstr. 24(4): 563 (4861).)

Nienstaedt, H.
1957. Silvical characteristics of white spruce (*Picea glauca*). U.S.D.A. Forest Serv. Lake States Forest Exp. Sta. Sta. Pap. 55, 23 pp., illus.

______ 1958. Receptivity of female strobili of white spruce. Forest Sci. 4: 110-115, illus.

______ 1961. Induction of early flowering: a critical review of recent literature. Recent Advances in Bot., Sect. 14: 1658-1662. Univ. Toronto Press.

Norin, B. N.
1958. (Germinative and vegetative reproduction of trees in wooded tundra). (Trans. by Israel Program for Scientific Translations for U.S. Dep. Agr. & Nat. Sci. Found. TT 65-50044. 99 pp., illus.)

Northern Forest Experiment Station.
1960-61. Biennial report. 28 pp., illus.

Northern Forest Experiment Station.
1962. Annual report. 24 pp., illus.

Parker, H. H.
1952. Spruce regeneration on deep moss after logging. Can. Dep. Resources & Develop. Forest. Br. Silvic. Leafl. 62, 2 pp.

Phelps, V. H.
1948. White spruce reproduction in Manitoba and Saskatchewan. Can. Dep. Mines & Resources, Dominion Forest Serv. Silvic. Res. Note 86, 32 pp., illus.

____
1949. Scarification to induce white spruce regeneration. Can. Dep. Mines & Resources, Dominion Forest Serv. Silvic. Leafl. 29, 2 pp.

____
1951. Survival of white spruce seedlings. Can. Dep. Resources & Develop. Forest. Br. Silvic. Leafl. 56, 2 pp.

Place, I. C. M.
1950. Comparative moisture regimes of humus and rotten wood. Can. Dep. Resources & Develop. Forest. Br. Silvic. Leafl. 38, 3 pp.

____
1955. The influence of seedbed conditions on the regeneration of spruce and balsam fir. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Bull. 117, 87 pp., illus.

Prochnau, A. E.
1963. Direct seeding experiments with white spruce, alpine fir, Douglas fir and lodgepole pine in the central interior of British Columbia. Brit. Columbia Forest Serv. Res. Note 37, 24 pp., illus.

Quaite, J.
1956. Survival of white spruce seedlings resulting from scarification in a partially cut mixedwood stand. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Forest. Res. Div. Tech. Note 44, 9 pp., illus.

Radvanyi, A.
1966. Destruction of radio-tagged seeds of white spruce by small mammals during summer months. Forest Sci. 12: 307-315, illus.

Roe, A. L.
1966. A procedure for forecasting western larch seed crops. Intermountain Forest & Range Exp. Sta. U.S.D.A. Forest Serv. Res. Note INT-49, 7 pp., illus.

Roe, E. I.
1963. Direct seeding of conifers in the Lake States: a review of past trials. Lake States Forest Exp. Sta. U.S.D.A. Forest Serv. Res. Pap. CS-3, 16 pp., illus.

Roe, E. I.
1946. Extended periods of seedfall of white spruce and balsam fir. U.S.D.A. Forest Serv. Lake States Forest Exp. Sta. Tech. Note 261, 1 p.

_____ 1948. Early seed production by balsam fir and white spruce. J. Forest. 46: 529.

_____ 1952. Seed production of a white spruce tree. U.S.D.A. Forest Serv. Lake States Forest Exp. Sta. Tech. Note 373, 1 pp.

Rowe, J. S.
1953a. Delayed germination of white spruce seed on burned ground. Can. Dep. Resources & Develop. Forest. Br. Div. Forest Res. Silvic. Leafl. 84, 3 pp.

_____ 1953b. Viable seed on white spruce trees in midsummer. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Div. For. Res. Silvic. Leafl. 99, 2 pp.

_____ 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Forest Res. Div. Tech. Note 3, 27 pp., illus.

Rudolph, T. D.
1965. The effect of gamma irradiation of pollen on seed characteristics of white spruce. *In* The use of induced mutations in plant breeding. Suppl. Radiation Bot., Oxford. pp. 185-191.

Sarvas, R.
1950. Effect of light on the germination of forest tree seeds. Oikos 2: 109-119.

_____ 1955. Investigations into the flowering and seed quality of forest trees. Metsäntutkimuslaitoksen Julkaisuja 45(7): 1-37, illus.

_____ 1957. Studies on the seed setting of Norway spruce. Meddelelser fra Det norske Skogforsøksvesen Nr. 48: 533-556, illus.

Scott, J. D.
1966. A review of direct seeding projects carried out by the Ontario Department of Lands and Forests from 1956 to 1964. Ontario Dep. Lands & Forests, Timber Br. Silvic. Notes 5, 48 pp., illus.

Scotter, G. W.
1963. Effects of forest fires on soil properties in northern Saskatchewan. Forest. Chron. 39: 412-421.

Silburn, George.
1960. Reforestation problems in western spruce forests, Forest. Chron. 36: 150-152, illus.

Silen, R. R.
1967. Earlier forecasting of Douglas fir cone crop using male buds. J. Forest. 65: 888-892, illus.

Smith, D. M.
1962. The practice of silviculture. Ed. 7, 578 pp., illus. New York: John Wiley & Sons, Inc.

Smith, F. H.
1958. Anatomical development of the hypocotyl of Douglas fir. Forest Sci. 4: 61-70, illus.

Smith, J. H. G.
1955. Some factors affecting reproduction of Engelmann spruce and alpine fir. Brit. Columbia Forest Serv. Dep. Lands & Forests, 43 pp., illus.

Stiell, W. M.
1955. The Petawawa plantations. Can. Dep. North. Aff. & Natur. Resources, Forest. Br. Forest Res. Div. Tech. Note 21, 46 pp., illus.

Tarrant, R. F.
1954. Effect of slash burning on soil pH. U.S.D.A. Forest Serv. Pacific Northwest Forest & Range Exp. Sta. Res. Note 102, 5 pp.

____
1956. Effects of slash burning on some soils of the Douglas fir region. Soil Sci. Soc. Amer. Proc. 20: 408-411, illus.

Timonin, M. I.
1964. Interaction of seed-coat microflora and soil microorganisms and its effect on pre- and post-emergence (survival) on some conifer seedlings. Can. J. Microbiol. 10(1): 17-22, illus.

____
1966. Effect of ultra-sound on the germination of white spruce and jack pine. Can. J. Bot. 44: 113-115.

Tiren, L.
1935. Om granens kottsättning, dess periodicitet och samband med temperatur ock nedebord (The cones-setting of spruce, its periodicity and relation to temperature and precipitation). Meddelanden fran Statens Skogsforsoksanstalt 28: 413-524. (Reviewed by P. O. Rudolf, J. Forest. 34: 444-445.)

Tripp, H. A., and Hedlin, A. F.
1956. An ecological study and damage appraisal of white spruce cone insects. Forest. Chron. 32: 400-410, illus.

Tucker, R. E., and Jarvis, J. M.
1967. Prescribed burning in a white spruce-trembling aspen stand in Manitoba. Woodlands Rev. 1967 (July): WR333-WR335.

U.S.D.A. Forest Service.
1948. Woody-plant seed manual. U.S. Dep. Agr. Misc. Pub. 654, 416 pp., illus.

Uggla, E.
1958. Ecological effects of fire on north Swedish Forests. Almquist and Wiksells Boktryekeri A. B. 18 pp., illus.

Uskov, S. P.
1962. On the fruiting of spruce stands. *In* Scientific basis for certain silvicultural measures in the northern part of the Vologda Region. Motovilov, G. P. (ed.) pp. 1-23. (Transl. from Russian. Israel Program for Scientific Translations. Jerusalem 1966. TT 65-50122.)

Vaartaja, O.
1963. Germination of white spruce seed not affected by extreme pH. Bi-mon. Rep. Forest Ent. Path. Br. Dep. Forest. Can. 19(3): 2-3.

Velkov, D., Ploscakova, L., Tilev, G.
1965. (Quality of Norway spruce seed in relation to site conditions.) Gorskostop. Nauka. Sofija. 2(1): 47-60 (In Russian.) (Forest. Abst. 28(3): 430 (35067).)

Wagg, J. W. B.
1963. Notes on food habits of small mammals in the white spruce forests. Forest. Chron. 39: 436-445, illus.

____
1964a. Viability of white spruce seed from squirrel-cut cones. Forest. Chron. 40: 98-110, illus.

____
1964b. White spruce regeneration on the Peace and Slave River lowlands. Can. Dep. Forest. Forest Res. Br. Pub. 1069, 35 pp., illus.

Waldron, R. M.
1961. Seeding white spruce at the base of aspen. Forest. Chron. 37: 224-233, illus.

____
1963. August-November seed and litter fall in a mature white spruce stand. Forest. Chron. 39: 333-334, illus.

____
1965. Cone production and seedfall in a mature white spruce stand. Forest. Chron. 41: 316-329, illus.

____
1966. Factors affecting natural white spruce regeneration on prepared seedbeds at the Riding Mountain Forest Experimental Area, Manitoba. Can. Dep. Forest. & Rural Develop. Pub. 1169, 41 pp., illus.

__________ and Cayford, J. H.
1967. Improved germination of white spruce by increasing moisture content with absorptive powders. Forest. Chron. 43: 149-154, illus.

Weetman, G. F.
1958. Forest seeding and planting techniques and equipment. Pulp & Pap. Res. Inst. Can. Tech. Rep. 74, 130 pp., illus.

Werner, R. A.
1964. White spruce seed loss caused by insects in interior Alaska. Can. Entomol. 96: 1462-1464.

Wilson, L. R.
1963. A study in variation of *Picea glauca* (Moench) Voss pollen. Grane Palynologica 4(3): 380-387, illus.

Winton, L. L.
1964a. Cessation of dormancy in white spruce. Minn. Forest. Note 155, 2 pp.

____
1964b. Meiosis and pollen release in white and black spruce and their hybrid. Minn. Forest. Note 154, 2 pp.

____
1964c. Phenology of normal and forced microsporogenesis in white and black spruce and their F hybrid. Minn. Forest. Note 153, 2 pp.

Woodwell, G. M.
1962. Effect of DDT on cone production, germination and seedling survival in the boreal forest. Ecology 43: 396-403, illus.

Zwolinski, M. J.
1967. Changes in water infiltration capacities following burning of ponderosa pine forest floor. (Abstr.) Dissert. Abstr. 27B(7), 2218.

Zasada, John C., and Gregory, Robert A.
1969. Regeneration of white spruce (*Picea glauca* (Moench) Voss) with reference to interior Alaska: a literature review. U.S.D.A. Forest Serv. Res. Pap. PNW-79, 37 pp. Pacific Northwest Forest & Range Exp. Sta., Portland, Oregon.

This paper reviews literature concerning natural regeneration of white spruce in the southern boreal forest and incorporates what is known about this subject for the boreal forests of interior Alaska. A mineral soil seedbed; reduction of competing vegetation; shade, especially during the first growing season; and an adequate seed supply are the four main regeneration requirements. Absence of a mineral soil seedbed appears to be the critical factor in the southern spruce forests.

Zasada, John C., and Gregory, Robert A.
1969. Regeneration of white spruce (*Picea glauca* (Moench) Voss) with reference to interior Alaska: a literature review. U.S.D.A. Forest Serv. Res. Pap. PNW-79, 37 pp. Pacific Northwest Forest & Range Exp. Sta., Portland, Oregon.

This paper reviews literature concerning natural regeneration of white spruce in the southern boreal forest and incorporates what is known about this subject for the boreal forests of interior Alaska. A mineral soil seedbed; reduction of competing vegetation; shade, especially during the first growing season; and an adequate seed supply are the four main regeneration requirements. Absence of a mineral soil seedbed appears to be the critical factor in the southern spruce forests.

Zasada, John C., and Gregory, Robert A.
1969. Regeneration of white spruce (*Picea glauca* (Moench) Voss) with reference to interior Alaska: a literature review. U.S.D.A. Forest Serv. Res. Pap. PNW-79, 37 pp. Pacific Northwest Forest & Range Exp. Sta., Portland, Oregon.

This paper reviews literature concerning natural regeneration of white spruce in the southern boreal forest and incorporates what is known about this subject for the boreal forests of interior Alaska. A mineral soil seedbed; reduction of competing vegetation; shade, especially during the first growing season; and an adequate seed supply are the four main regeneration requirements. Absence of a mineral soil seedbed appears to be the critical factor in the southern spruce forests.

Zasada, John C., and Gregory, Robert A.
1969. Regeneration of white spruce (*Picea glauca* (Moench) Voss) with reference to interior Alaska: a literature review. U.S.D.A. Forest Serv. Res. Pap. PNW-79, 37 pp. Pacific Northwest Forest & Range Exp. Sta., Portland, Oregon.

This paper reviews literature concerning natural regeneration of white spruce in the southern boreal forest and incorporates what is known about this subject for the boreal forests of interior Alaska. A mineral soil seedbed; reduction of competing vegetation; shade, especially during the first growing season; and an adequate seed supply are the four main regeneration requirements. Absence of a mineral soil seedbed appears to be the critical factor in the southern spruce forests.

Headquarters for the PACIFIC NORTHWEST FOREST AND RANGE EXPERIMENT STATION is in Portland, Oregon. The Station's mission is to provide the scientific knowledge, technology, and alternatives for management, use, and protection of forest, range, and related environments for present and future generations. The area of research encompasses Alaska, Washington, and Oregon, with some projects including California, Hawaii, the Western States, or the Nation. Project headquarters are at:

College, Alaska	Portland, Oregon
Juneau, Alaska	Roseburg, Oregon
Bend, Oregon	Olympia, Washington
Corvallis, Oregon	Seattle, Washington
La Grande, Oregon	Wenatchee, Washington

The FOREST SERVICE of the U.S. Department of Agriculture is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives — as directed by Congress — to provide increasingly greater service to a growing Nation.